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ESTIMATING BIOGEOCHEMICAL FLUXES ACROSS
SAGEBRUSH-STEPPE LANDSCAPES WITH THEMATIC MAPPER IMAGERY

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ABSTRACT

Thematic Mapper (TM) satellite data were coupled to an ecosystem simulation model to simulate variation in nitrogen mineralization over time and space in a sagebrush steppe. This system of data inputs and calculations provides estimates of ecosystem properties including rates of biogeochemical processes over extensive and complex landscapes, and under changing management and climatic conditions. Efforts to measure late-spring snow cover and distribution, the major source of soil moisture in this semi-arid system, failed because of insufficient frequency of satellite overpasses at this cloudy time of year.

INTRODUCTION

This paper reports partial results of a project designed to assess ecosystem properties over complex terrain of sagebrush steppe by means of Thematic Mapper (TM) imagery. Ecosystem properties of interest were the distribution of vegetation and soil nutrient pools over the landscape and certain biogeochemical processes. Processes addressed in this overall study included N-mineralization, nitrification, nitrous oxide efflux and erosion; this paper is restricted to the first of these.

N-mineralization is a measure of the rate and amount of nitrogen made available for plant and microbial utilization. Because nitrogen is often a limiting resource in terrestrial ecosystems when temperature and moisture are non-limiting, this nitrogen supply rate at times represents the limiting resource for plant growth and primary production. In this system, most of the nitrogen mineralized is in the nitrate form (Burke 1987,

1988). Nitrate availability is of interest for many reasons, one of which is its potential conversion to volatile forms of nitrogen, especially nitrous and nitric oxides (Matson 1987). These two gases are important in terms of their contribution to the earth's greenhouse effect and ozone reactions in the atmosphere (Crutzen 1983, Mooney et al. 1987). One of the uses of the application described here is an assessment of the production and efflux of these gases over space and time under both natural conditions and scenarios of climate change (Coppinger et al. 1988). For these reasons, N-mineralization is a keystone process and was chosen as the central focus of this work.

Sagebrush steppe is a North American form of semi-desert occurring in a temperate, semi-arid climate with mainly winter precipitation, and with a plant cover consisting of mixtures of shrubs, mostly of the genus Artemisia, together with grasses and forbs (West 1983a). Sagebrush steppe comprises $0.45 \times 10^6 \text{ km}^2$, and a related type, the sagebrush semi-desert, collectively comprise $0.62 \times 10^6 \text{ km}^2$ in the western U.S. (West 1983b). Analogous deserts and semi-deserts of Eurasia comprise another $4.92 \times 10^6 \text{ km}^2$ (West 1983c) so that together, these deserts and semi-deserts represent a significant fraction of the earth's land surface. Changes in land use (West 1983a) or climate (NRC 1986) over the vast areas dominated by sagebrush may influence changes in biospheric function through a number of biogeochemical and biogeophysical roles.

Within sagebrush steppe there is considerable variation

throughout its geographic range (West 1983a), or, in complex terrain, even at the scale of a first-order watershed. It is important to assess this variability in order to understand the relationships between driving variables and processes, to assess the influence of one part of the landscape on another, and to accurately extrapolate process rates over larger areas, for longer times, and for novel conditions. TM imagery with its fine spatial resolution and synoptic coverage is an excellent tool for achieving these goals. The objectives described in this paper were to develop a functional classification of ecosystem types across this landscape and to estimate N-mineralization rates over time and space through the use of an ecosystem simulation model parameterized for each ecosystem type.

METHODS

Study Area

The study area was restricted to a section of Browns Park Formation (Miocene) in south-central Wyoming to gain uniformity in the general climatic patterns, geomorphological processes, soil types, and the relationships of vegetation and soils with land form (Fig. 1). Much, but not all of the work was centered on the Stratton Sagebrush Hydrology Study Area (SSHSA) (Fig. 1), where long-term climatological and other data, plus site security were available (Sturges 1978, 1982). Terrain in this area is gently rolling, with about 100 m of relief and an average elevation of 2400 m. Soils typically have a loamy sand texture and most are classified in the Argic Cryoboroll great group (Sturges 1986). Soils are deepest and best developed in

areas of snow accumulation and are shallow and poorly developed on dry, windswept ridges (Evans (1987), Burke et al. (1988), Burke 1988). Summers at SSHSA are cool and winters long and cold; the average annual temperature is 2.7°C (Sturges 1986). Annual precipitation at SSHSA averages 525 mm with 75% of this falling as snow (Sturges 1986). This area occupies the cool, wet end of the spectrum of conditions for sagebrush steppe in Wyoming. Of special importance in this environment are strong winter winds which redistribute snow across the rolling terrain, (January mean = 8.3 m s⁻¹ (Sturges 1982)) creating a very complex pattern of soil moisture, and thus plant and soil features across the landscape (Sturges 1977, 1978). This complexity challenges the spatial resolution of TM.

Areas of deepest snow accumulation, where sagebrush species cannot persist, are dominated by grasses and forbs. Along drainages and on leeward slopes where snow accumulations are moderate to deep, Artemisia tridentata ssp. vaseyana (mountain big sagebrush) is the dominant species often mixed with Festuca idahoensis. On slightly drier slopes, the shorter subspecies of Artemisia tridentata, ssp. wyomingensis, (Wyoming big sagebrush) predominates. As snow accumulation and soil moisture decrease with position on windward slopes, Artemisia nova (black sagebrush) a short, nearly prostrate shrub, mixes with cushion-forming plants. The most windswept, and thus, driest ridges are characterized by a sparse vegetation cover of cushion plants (Burke 1988).

Two objectives were pursued with regard to remote sensing: 1) to develop a relationship between TM reflectance factors and vegetation and soil characteristics in order to classify and map sagebrush ecosystems, and 2) to map snow cover--a critical environmental variable in this system that could be used to index annual variation in soil moisture recharge.

Thematic Mapper Data

Landsat-5 Thematic Mapper data were obtained for quadrants 3 and 4 of row 31, path 35 for 11 cloud-free acquisitions during late spring-early summer in 1985, 1986 and 1987. The data were radiometrically and geometrically processed "P" data with cubic convolution resampling to 28.5 m square pixels in the UTM projection. Coefficients for scene-to-scene registration were estimated using the block correlation method (Schowengardt 1983). Inspection of the images and the correlation results revealed accurate scene-to-scene registration (within 1 pixel) was possible using simple column offsets. This suggests the "P" data geometric correction was made without the use of geodetic control data (NASA 1984).

The observations obtained from TM are mid-morning nadir-view hemispherical-conical measurements of reflected and emitted radiance. The reflectance factor (RF) used in this paper is similar in form to the reflectance factor presented by Richardson et al. (1980):

$$RF = \frac{(L-L_p)}{\frac{E_{sun}}{d^2} * \cos \phi_{sun} * T_{oz} * T_{ray+oz}}$$

where

L = Spectral radiance at sensor aperture ($\text{mW cm}^{-2} \text{ sr}^{-1} \mu\text{m}^{-1}$)
 L_p = Rayleigh Path radiance ($\text{mW cm}^{-2} \text{ sr}^{-1} \mu\text{m}^{-1}$)
 E_{sun} = Mean solar exoatmospheric irradiance ($\text{mW cm}^{-2} \mu\text{m}^{-1}$)
 d = Earth-Sun distance (Astronomical units)
 ϕ_{sun} = Solar zenith angle (degrees)
 T_{oz} = Transmittance through ozone from sun to surface
 $\quad = \exp(-t_{\text{oz}}/\cos \phi_{\text{sun}})$
 $T_{\text{ray+oz}}$ = Transmittance through rayleigh and ozone
 \quad atmosphere from surface to sensor
 $\quad = \exp((-t_{\text{oz}} + -t_{\text{ray}})/\cos \phi_{\text{sensor}})$
 t_{ray} = Rayleigh optical depth
 t_{oz} = Ozone optical depth
 ϕ_{sensor} = Sensor zenith angle

Calibration coefficients for converting relative spectral response to spectral radiance at the sensor, and mean solar exoatmospheric irradiances in the TM bands were obtained from Markham and Barker (1987). Solar zenith angle was calculated using the latitude and longitude of the SSHSA and satellite overpass time. Rayleigh path radiance was estimated using equation 2 of Gordon et al. (1983). Rayleigh optical depth was estimated for the TM visible and near infrared bands using Frohlich and Shaw's (1980) equation with the depolarization correction factor of Young (1980). Ozone optical depth was estimated for the visible bands using the average of ozone molecule cross section taken at 5 nm intervals within a band, and an ozone concentration of 300 Dobson units (WMO 1985).

The reflectance factor is a first approximation of radiative transfer for a Lambertian surface imaged under conditions of a minimal atmosphere in which Rayleigh scattering and ozone

absorption are always present (Otterman and Robinove 1981). Rayleigh optical depth was omitted from the calculation of transmittance from the sun to the surface since most of the radiation removed from the direct irradiance becomes diffuse irradiance (Ahern et al. 1977). The reflectance factor does not include the effects of multiple and Mie scattering, or water vapor absorption, the latter being particularly important for the mid-infrared bands (Slater et al. 1987). We would have preferred to develop reflectance transformations with TM data using methods of Crippen (1987), Volchok and Schott (1986), or Ahern et al. (1977), however, the environmental characteristics of our study area were not amenable to these methods. Classifying and Mapping the Sagebrush Steppe

Observations of the autecology and synecology of sagebrush in the Wyoming Basin (Sturges 1977, 1978), and vegetation and soil process studies at the SSHSA (Burke 1988) provided the basis for identification and classification of sagebrush ecosystems. A field reconnaissance of the SSHSA was performed using 1:30,000 scale, color infrared photographs, soil maps and topographic maps. Polygons of relatively homogeneous vegetation were delineated on the 1:30,000 scale photographs, and observations of dominant species, height and cover of vegetation, soil surface color and relative amounts of bare soil, gravel and rock recorded.

Our goal was to identify sagebrush ecosystems larger than the spatial resolution of the TM, thus we used discrete classification methods to map sagebrush ecosystems. Development

of reflectance factor statistics for sagebrush ecosystems began with unsupervised euclidean distance clustering of the six optical TM bands and maximum likelihood classification of a 500 by 500 pixel subsection from the June 7, 1985 TM image containing the SSHSA (Fig 2). Relationships between unsupervised spectral classes and sagebrush ecosystems were established by correspondence of spectral classes with the field reconnaissance data. Using the relationships between spectral classes and undisturbed sagebrush ecosystems developed at the SSHSA, a classified image was prepared for sagebrush steppe occurring on the Browns Park Formation. The Geologic Map of Wyoming (Love and Christiansen 1985) was used to delineate the general outline of the Browns Park formation in the TM data by excluding protrusions from the north of adjacent Cretaceous formations, and establishing southern boundaries along the points of contact with the North Park Formation, Sierra Madre Mountains, and the sagebrush steppe-aspen ecotone having distinctly different characteristics on the west side of the mountains (Fig. 1). Field reconnaissance examined the relationships of spectral classes and sagebrush ecosystems as the extent of the study area and disturbance of sagebrush ecosystems increased.

Supervised training was introduced into the procedure when complex spectral classes (corresponding to more than one sagebrush type) were identified in the evaluation of the emerging classified image. The TM data for pixels of complex spectral classes were reclustered and additional spectral classes generated. The maximum likelihood classification was then

repeated using revised spectral class statistics, and through this process of successive approximations, a set of spectral classes corresponding to sagebrush ecosystems developed.

This successive approximation yielded a statistics file containing 88 spectral classes from the June 7, 1985 TM image. The 88 spectral classes were combined into 27 spectral classes on the basis of similarity in land cover. Inspection of the 27 class image revealed a high frequency grain related to canopy characteristics rather than the vegetation-soil complexes themselves. This fine spatial structure in the image resulted from the maximum likelihood decision rule that classifies each pixel independently without reference to adjacent pixels. The 27 class image was spatially filtered in a 3-step process to reduce this undesirable, fine spatial structure in the image. The process involved a region-labeling algorithm that constructed pseudo-polygons from contiguous pixels of the same class (Nichols 1981), the assignment of a null label to all polygons smaller than three pixels, and neighborhood filtering to assign pixels with null labels to the class of adjacent pixels.

Another error, the misclassification of graminoid-dominated ecosystems as sagebrush ecosystems using only the June 7, 1985 TM scene, was also apparent. The change in spectral reflectance associated with increase in green phytomass of the graminoid ecosystems between the June 7 and July 9, 1985 TM images was used to reduce these commission errors for sagebrush classes. The Perpendicular Vegetation Index and Soil Line Index (Richardson and Wiegand 1977) were calculated from reflectance factors for TM

bands 3 and 4 from the June 7 and July 9, 1985 TM images and used to calculate a vector describing the distance and angle of change for each pixel (Malia 1980). The change vector images were compared with field reconnaissance observations and aerial photography. Pixels exceeding a distance of 4.0 and having angles between 1-90 degrees were reclassified into the graminoid landcover class.

After spatial filtering and change vector analysis, the 27 spectral classes were generalized into three sagebrush ecosystems and another class representing all other cover types. This was required to accomodate the constraints of model parameterization which could only be generalized for these limited classes.

Mapping Snow Cover

Accurate mapping of snow cover could not be achieved due to an inability to obtain suitable TM images in late spring in 1985, 1986, and 1987. Cloud cover generally prevented acquisition of useable TM images although conflicts with use of the data relay satellite and conflicts with receiving station operations also played a role. The 16 day repeat coverage provided by a single Landsat satellite appears inadequate to reliably obtain images of snow coverage in late spring prior to initiation of snow melt for this system. Identification of snow cover is simple, however, so that if more frequent imagery of comparable resolution could be obtained, we could enhance the usefulness of the TM-driven simulation model system developed in the project.

Adaptation of the CENTURY Model

The original objective for this research was to predict,

from TM information alone, spatial and temporal variation in vegetation type, vegetation biomass, soil properties and N-mineralization rates. Two critical driving variables could not be provided by TM, however--soil temperature and snow cover (and thus derived soil moisture. Consequently, TM data are used to provide areal definition for soil-vegetation conditions within the defined study area, and ground-derived estimates of temperature and soil moisture are used to drive a simulation model that estimates N-mineralization. The ecosystem simulation model used in this study was adapted from the CENTURY model described by Parton et al. (1987, 1988a) (Fig. 3). Essentially, the model simulates the flux of carbon, nitrogen and other elements from live plants, to plant residues, through three functional forms in soil organic matter, to available inorganic pools, and back to plants. The model includes complex element interactions, such that C and N pools and transformations constrain one another. Atmospheric inputs and outputs are also modeled.

Precipitation and nutrient availability are the principle controls on plant production in the model. Decomposition and mineralization are driven by a composite "climate decomposition parameter" which is calculated from temperature and precipitation data. Chemical properties of the residue, particularly the lignin/nitrogen ratio and soil texture, control the rate of carbon and nitrogen release from plant residues. Data needed for driving variables include monthly averaged maximum and minimum air temperatures, monthly averaged precipitation, and soil

texture (Fig. 3). The nitrogen budget includes inputs via precipitation and volatile losses of N_2O via both nitrification and denitrification. Nitrogen input was estimated from a simple regression equation relating effective precipitation to atmospheric nitrogen inputs derived from National Atmospheric Deposition Program data sets; gaseous outputs were calculated as described by Parton et al. (1988b). Values used in this adaptation of CENTURY to sagebrush steppe are listed in Table 1. Plant root to shoot ratios were taken from field measurements (unpublished data) and plant lignin/nitrogen ratios were derived from data collected by Parton et al. (1987). Soil texture, carbon and nitrogen were measured at SSHSA (Burke 1988, Burke et al. 1988). Annual effective precipitation estimates were derived from measurements of snow deposition on landscape positions correlating with the three sagebrush types (Sturges 1977a). Monthly temperature values were derived from D.L. Sturges, unpublished data. Initial outputs from CENTURY were tested by comparing monthly microbial biomass and rates of N-mineralization simulated by 1985 weather conditions with observed field data from taken in the same year. CENTURY was adjusted according to the resulting deviations to more accurately simulate field measurements. Model output described in the following results is for 1986. These outputs were applied to areal coverage by the three main sagebrush types as defined by remote sensing analysis.

RESULTS AND DISCUSSION

Remote Sensing

Three composite sagebrush vegetation types together with a

composite of other types are illustrated in the classified image (Fig. 4). The three sagebrush types correspond to aggregations of species found along an environmental gradient of effective precipitation. The types vary from mesic, high snow deposition sites dominated by Artemisia tridentata subsp. vaseyana (ARTRVA), to intermediate levels of soil moisture recharge at mid-slope positions dominated by A. tridentata subsp. wyomingensis (ARTRWYO), to xeric, windswept upper slopes and ridges with low snow accumulation dominated by A. nova (ARNO).

The same mesic-xeric gradient found locally is also reflected in larger scale in Fig. 4. More of the landscape is dominated by ARNO to the east, more by ARTRVA on the west, while ARTRWYO falls into an intermediate position. This large scale gradient represents an increase in effective soil moisture through an increase in elevation from east to west, possibly an orographic effect of the Sierra Madre Mountains on precipitation, and possibly to a diminution of wind on the west side of the mountains. On the west side of the mountains, Artemisia tridentata subsp. vaseyana is the climatic climax occupying most upland positions, whereas on the east side of the mountains, it is only a topographic climax found in snow deposition sites.

Discrimination of vegetation-soil ecosystems using spectral reflectance measurements requires that ecosystems be composed of elements with different spectral properties, different proportions of the same elements, or different geometric arrangements of the elements. The ARTRVA type was spectrally distinctive because of greater canopy coverage and height of

sagebrush, greater canopy coverage of grasses; and a dark, grayish-brown, soil surface. Dark soil allowed discrimination of disturbed ARTRVA ecosystems from ARTRWYO and ARNO sagebrush ecosystems which have light brown, gravelly soil surfaces. Artemisia tridentata subsp. wyomingensis often assumes a decumbent growth form similar to that of A. nova which prevented reliable discrimination of areas dominated by each species. The ARTRWYO and ARNO sagebrush ecosystems recognized in the TM classification correspond to a gradient in canopy coverage and phytomass and soil surface characteristics rather than to species composition itself. Given the difficulty in reliably separating ARTRWYO- and ARNO-dominated vegetation cover, and given the general predominance of A. tridentata subsp. wyomingensis, the best conservative designation on a TM scale map depicting species dominance would be ARTRWYO.

Coupling Model Output and Ecosystem Types Across the Landscape

Estimates of N-mineralization for each sagebrush ecosystem type were simulated for each month of 1986. These rates were multiplied by the areas of each type in the delineated study area to give total N-mineralization for each month, and cumulatively, for the year. In general, rates are highest in late spring-early summer, then decline through the summer and are very low over the winter months. Rates for only two months and the annual total are given in Table 2. June and August rates are illustrated because June has very high rates for the mountain big sagebrush type (ARTRVA) and August has quite low rates for all

types because of summer drying of the soil.

The percent contributions by each of the types to available N pools in the entire, classified landscape are given in Table 3. Although ARTRVA covers only 42% of the area dominated by these three types, it accounts for 59% of total N-mineralization. Any change in the area occupied by this type, whether through human intervention or climate change, would invoke a large change in nitrogen cycling for the entire landscape. Extrapolation of these results over the full range of sagebrush steppe, or even the sagebrush-dominated basins of Wyoming, would best be done with some accounting for the relative distributions of three main ecosystem types. As noted earlier, this study area lies on the mesic end of a spectrum of environmental conditions and the ARTRVA type is probably more prominent here than over most of the sagebrush steppe of Wyoming where the ARTRWYO type predominates.

The intensity of N-mineralization for these three time periods is shown with a linearized gray scale for rates in the composite Fig. 5. Clearly, there is considerable variation in the spatial and temporal distribution of this biogeochemical process which is both a product and contributor to the variability in other ecosystem properties of this complex landscape.

SUMMARY

This paper reports on part of the results from a project addressing the use of remote sensing to predict biogeochemical processes across sagebrush steppe. N-mineralization rates were calculated from a simulation model based on terrain

interpretation from TM imagery. Limitations on parameterization of the model for all recognizable classes of vegetation-soil types on the landscape did not permit use of the full degree of resolution possible by TM imagery. With more work on parameter estimation, better spatial resolution of biogeochemical processes will be possible.

The low frequency of TM overpasses and high frequency of cloud cover, even in this semi-arid region, prevented the estimation of snow cover by TM, and from that, estimation of effective soil moisture. Had such data been available, most aspects of N-mineralization, and other biogeochemical processes, could be estimated over the complex sagebrush steppe landscape with inputs of driving variables from TM alone.

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Table 1. Values used to modify the CENTURY model for simulating behavior in sagebrush steppe of south-central Wyoming.

Value	ARTRVA	ARTRWYO	ARNO
Root/shoot ratio	0.9	1.3	1.5
Lignin/N ratio			
aboveground	0.85	0.14	0.13
belowground	0.118	0.21	0.22
Soil texture			
sand (%)	75	78	78
silt (%)	15	12	12
clay (%)	10	10	10
Soil carbon (0-15 cm, g m ⁻²)	3000	2600	2700
Soil nitrogen (0-15 cm, g m ⁻²)	310	275	260
Annual effective precipitation (cm)	53.8	35.6	28.3
Annual N-input via precipitation (g m ⁻²)	1.0	0.7	0.55

Table 2. Areas and predicted N-mineralization rates for the three major ecosystem types of the Browns Park Formation of south central Wyoming. The total area of Browns Park Formation as delineated in Fig. 2 is 932.6 km². The sum of area for other The sum of area for other vegetation types (Aspen, riparian, upland graminoid, irrigated hayfields, bitterbrush, mountain shrub communities and others) is 193.9 km². The area of water in the June 7, 1985 TM scene is 3.7 km².

Sagebrush Ecosystem Type*	Area within Browns Park Formation as Delineated (km ²)	Net N-mineralization			Net N-mineralization		
		June	August (kg ha ⁻¹)	Annual	June (tonnes)	August	Annual
ARTRVA	310.42	10.7	5.9	22.5	332.8	183.1	698.4
ARTRWYO	181.98	3.2	1.8	11.8	57.9	33.5	214.7
ARNO	242.57	2.8	1.8	10.8	67.9	43.7	262.0
Sum	734.97			sum	458.6	260.3	1175.1

*ARTRVA is the symbol for the ecosystem type dominated by Artemisia tridentata subsp. vaseyana, ARTRWYO represents the type dominated by A. tridentata subsp. wyomingensis, ARNO represents the type dominated by A. nova.

Table 3. Percent contribution of major ecosystem types of the Browns Park Formation of south central Wyoming to area and to total N-mineralization as predicted by the CENTURY MODEL on three time periods, the full year, June and August, 1986.

Ecosystem type	% of Sagebrush Ecosystems	% Annual	% June	% August
ARTRVA	42.2	59.4	72.6	70.3
ARTRWYO	24.8	18.3	12.6	12.9
ARNO	33.0	22.2	14.8	16.8
ARTRWYO + ARNO	57.8	40.6	27.4	29.6

FIGURES

Fig. 1. Map of portion of south central Wyoming in which the research was conducted. The area represented by these results is restricted to the Browns Formation which is bounded on the north by the several Cretaceous formations and on the south by the Sierra Madre Mountains and North Park Formation. The Stratton Sagebrush Hydrology Study Area where much of the ground work took place is shown in black.

Fig. 2. A color composite image derived from TM data of June 7, 1985. Bands TM5 (1.55-1.75 μm), TM4 (0.76-0.90 μm) and TM3 (0.63-0.69 μm) are displayed through red, green and blue filters, respectively. The image subsection used to develop relationships between TM reflectance factors and sagebrush ecosystems is outlined in upper center. Representatives of five shrub dominated ecosystems are identified in the subsection with white letters. A - mountain big sagebrush, B - Wyoming big sagebrush, C - black sagebrush, D - black sagebrush with bright soil, E - bitterbrush.

Fig. 3. General structure of CENTURY, a simulation model for soil processes in grasslands adapted for sagebrush steppe. See text for explanation.

Fig. 4. A classified image of the major ecosystem types of sagebrush steppe on the Browns Park Formation within the subsection defined in Fig. 2. See Fig. 1 for delineation of the

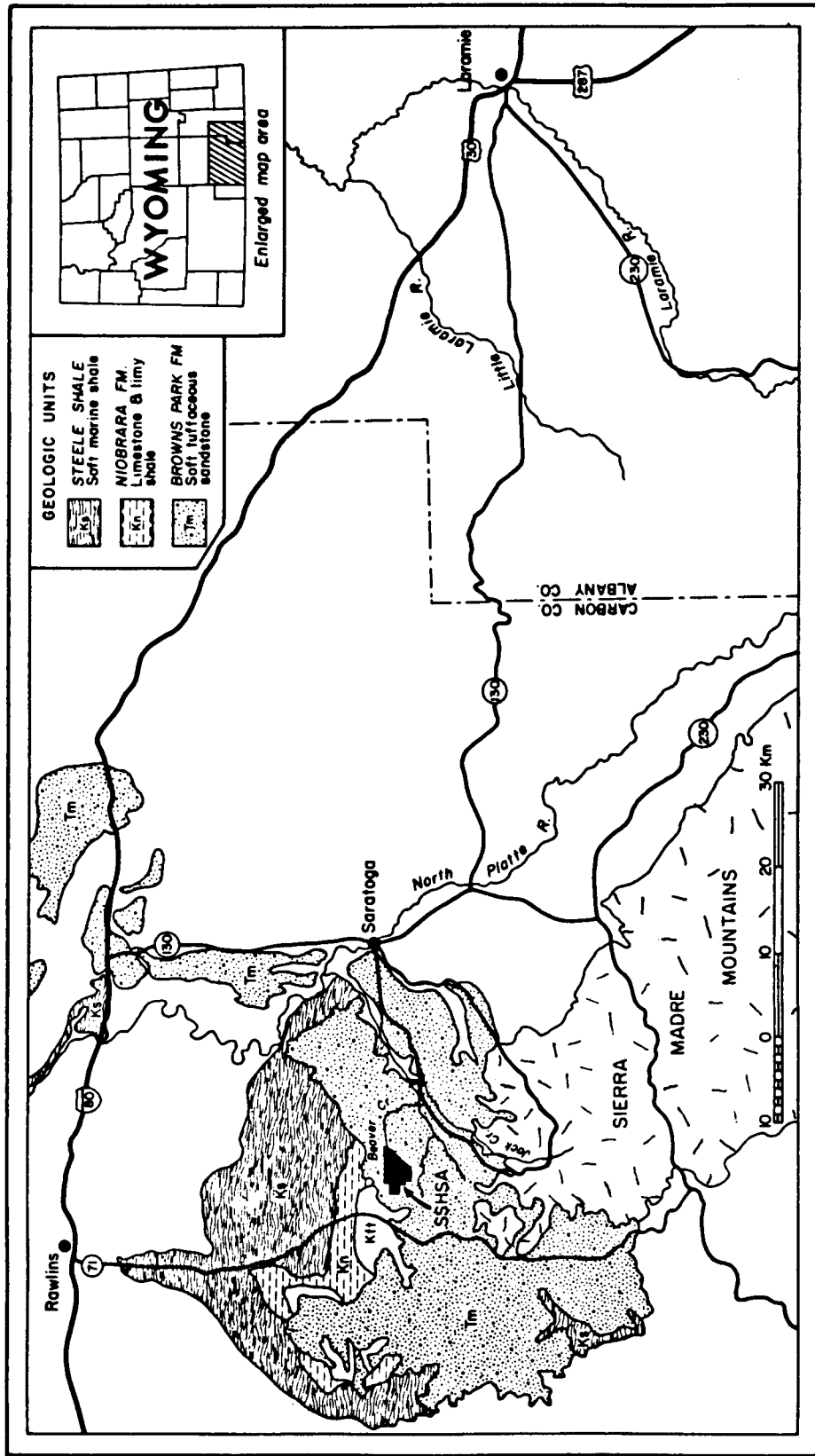
Browns Park Formation in this area. The five types listed in Fig. 1 have been decreased to three types. Type D in Fig. 2, "Black Sagebrush with bright soil", has been pooled with type C, "Black sagebrush". Type E has been deleted from this classified image and is shown in black along with riparian and other non-sagebrush types. The three main types are represented as follows: green - mountain big sagebrush (ARTRVA), light brown - Wyoming big sagebrush (ARTRWYO), sand - black sagebrush (ARNO).

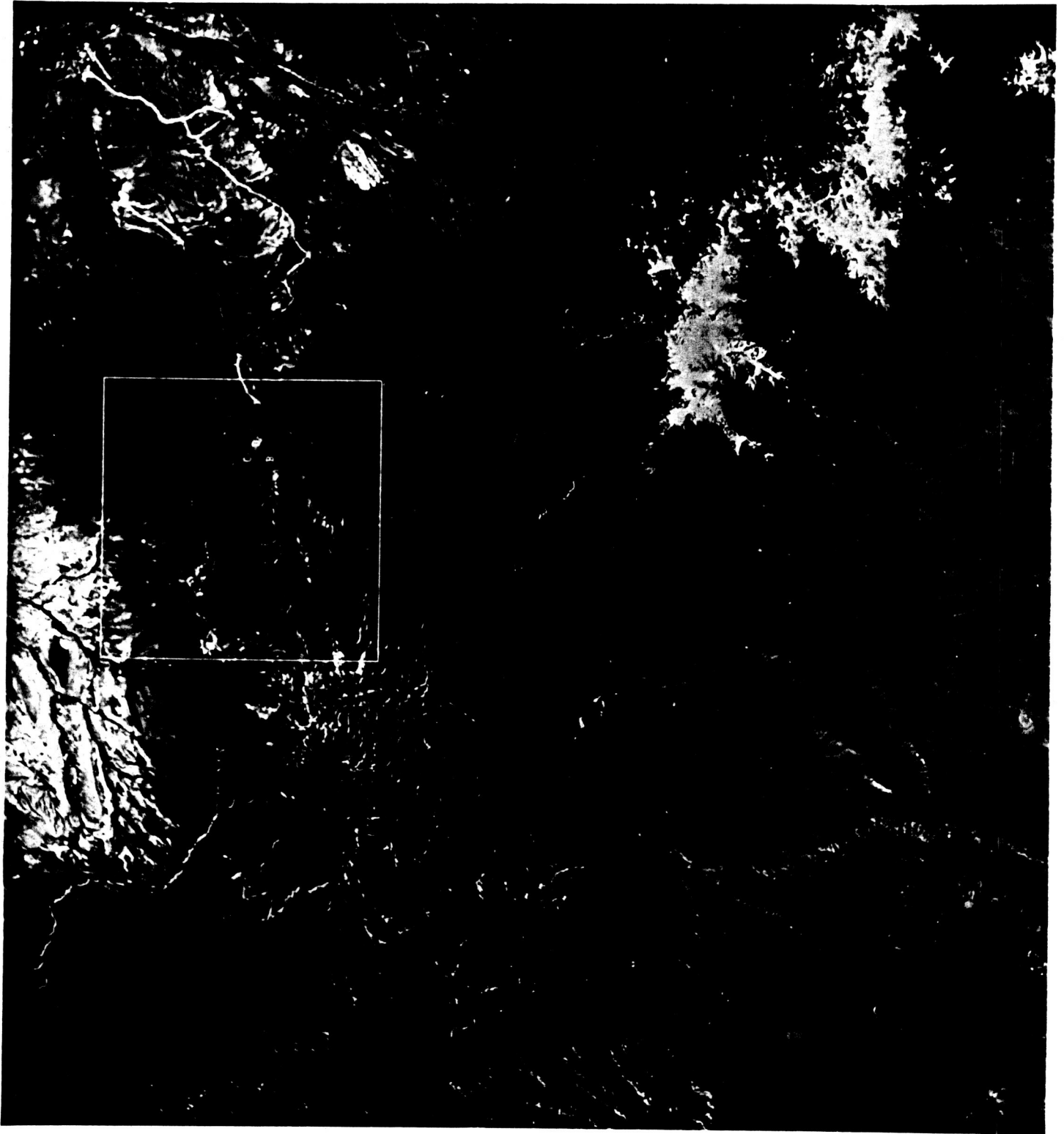
Fig. 5. Net N-mineralization by the three main sagebrush ecosystems of the Browns Park Formation in south central Wyoming.

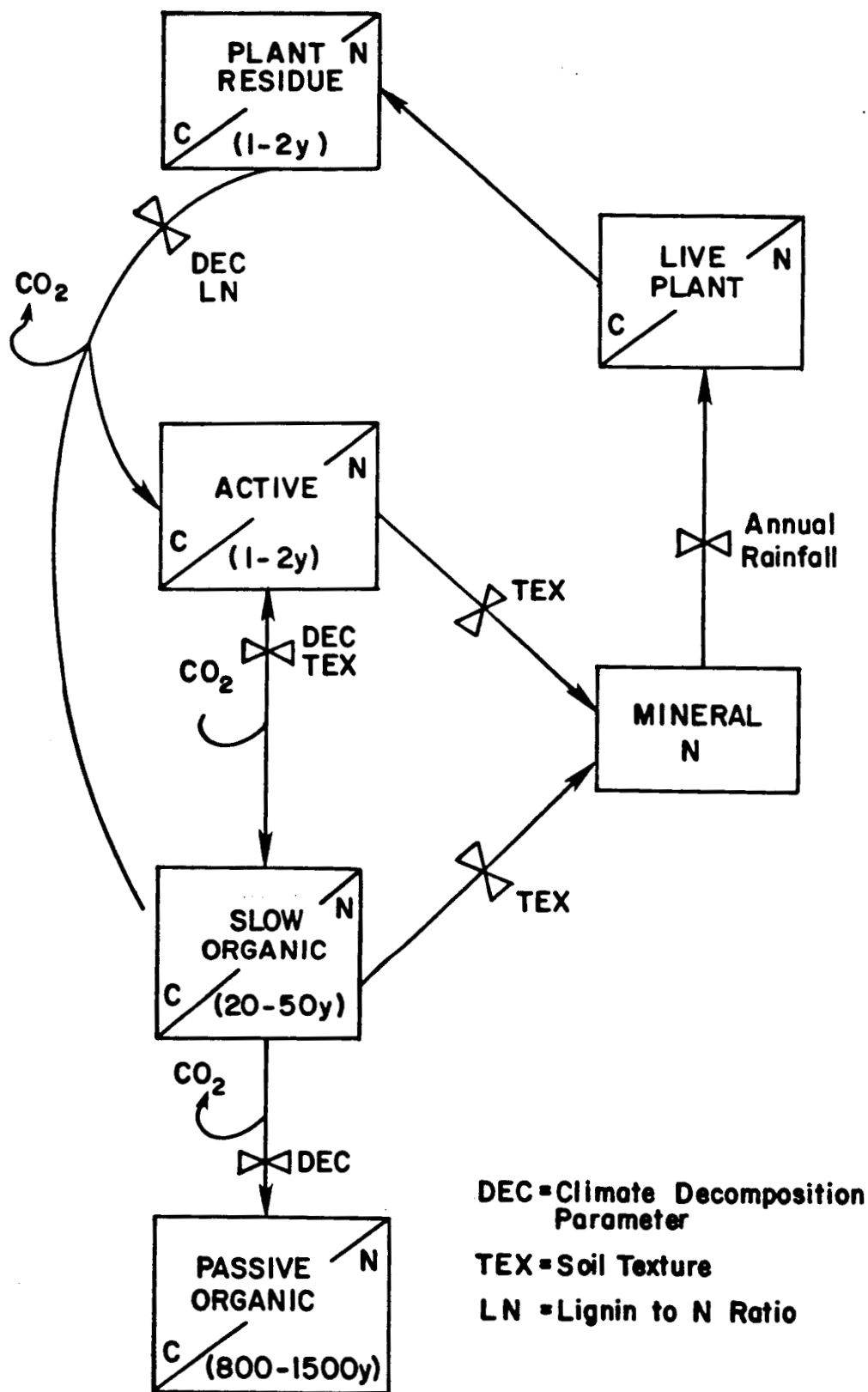
A--Annual net N-mineralization (linear grey scale varies from
1.08 to 2.25 g N m⁻²

B--June net N-mineralization (linear gray scale varies from
0.18 to 1.072 g N m⁻²

C--August net N-mineralization (same linear gray scale as
June).

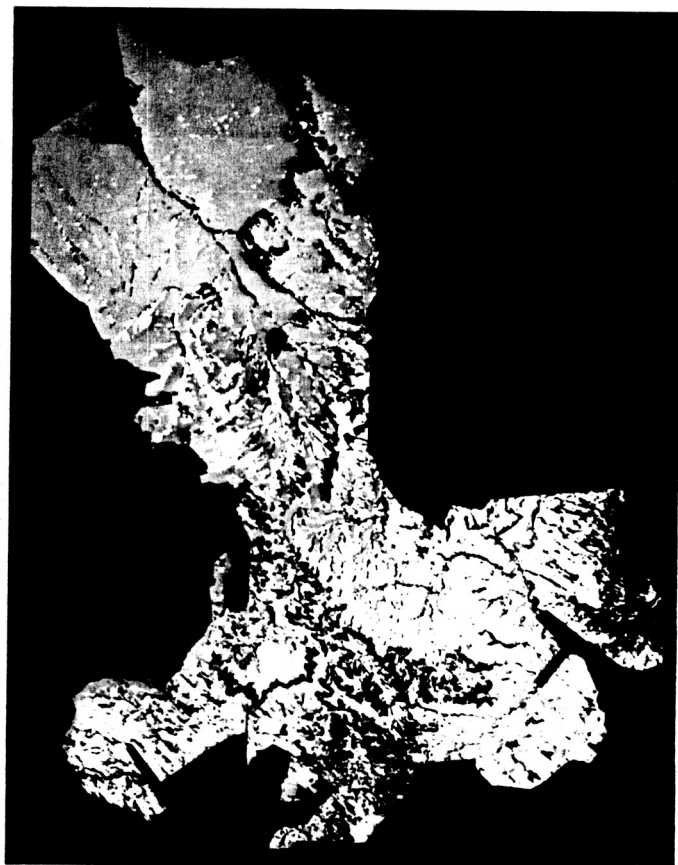








B



C

A

